

# The life-history traits of *Eurycea guttolineata* (Caudata, Plethodontidae), with implications for life-history evolution

Jeremy L. MARSHALL<sup>1-2</sup>

Department of Biology, University of Southwestern Louisiana,  
P.O. Box 42451, Lafayette, Louisiana, 70504-2451, USA  
E-mail: jmarshal@usl.edu

Evaluating life-history traits allows for the assessment of local adaptation and its correlated fitness consequences. The goal of this study was to describe the life-history traits of a spring-dwelling population of *Eurycea guttolineata* to gain a better understanding of life-history evolution in the Plethodontidae. Size at first reproduction,  $\geq 50.00$  mm SVL, was similar between males and females and was attained at 22-24 months of age. However, a larger variance in size of sexually mature females (about twice male variance) may suggest that some females do not become sexually mature until 34-36 months of age. The data suggest a period of sexual activity from late summer to early winter (July-December), ovipositing occurring in early winter (November-December), and egg hatching probably occurring in January or February. During ontogeny, growth rates were high during the first (2.48 mm SVL/mon) and second (1.70 mm SVL/mon) years, but decreased (0.11 mm SVL/mon) once sexual maturity was reached. I found that metamorphosis occurred typically in June, at a size of 23.08 mm SVL, at 5-6 months of age. A coefficient of variation analysis revealed that age at metamorphosis was significantly more variable than size. This, in conjunction with the fast larval growth rates and short larval period of this species, is consistent with a hypothesis based on larval adaptation to warm, stable aquatic environments in which an optimal size at metamorphosis is reached at an early age. This analysis does not support the hypothesis that larvae of this species are adapted to uncertain environments.

## INTRODUCTION

Evaluating life-history traits across the geographic distribution of a species is critical to interpreting the influence of local environments on life-history variation (STEARNS, 1992, TILLY & BERNARDO, 1993). Such variation in life-history traits may reflect phylogeny

1 Work completed at Department of Biology, University of Mississippi, University Mississippi 38677, USA

2. This paper is dedicated to the memory of Nick PIETROPAOLO.

(HARVEY & PAGEL, 1991) or may represent adaptation to local environments (LEVINS, 1968, STEARNS, 1992). Life-history studies that address phylogenetic history and local adaptations are now being conducted at the level of genus and species with comparative methods (BAUWENS & DIAZ-URIARTE, 1997; IRSCHICK & LOSOS, 1998). However, a fundamental criterion for evaluating the evolution of life-history traits, with comparative methods, is that such traits are known for each of the taxa or populations under consideration (HARVEY & PAGEL, 1991).

Life-history traits of the genus *Eurycea* (Caudata, Plethodontidae) have been documented from across the eastern United States (*E. longicauda*, ANDERSON & MARTINO, 1966; *E. multiplicata*, IRELAND, 1974; *E. quadridigitata*, SEMLITSCH & McMILLAN, 1980, *E. junaluska*, SEVER, 1983; *E. wilderae*, BRUCE, 1988; *E. cirrigera*, MARSHALL, 1997; *E. lucifuga*, CARLYLE et al., 1998). Considerable intraspecific variation in life-history traits has been observed, especially within those species that inhabit a wide variety of habitats (TILLEY & BERNARDO, 1993; VOSS, 1993, MARSHALL, 1996, 1997, CARLYLE et al., 1998). Habitat differences are the impetus for local adaptation and may lead to the evolution of novel life-history characteristics (e.g., BAHERT, 1996; MARSHALL, 1996). Therefore, the assessment of life-history traits among closely related species or populations within different habitats and regions should illuminate potential sources of life-history variation (BERVEN, 1982; TILLEY & BERNARDO, 1993).

The three-lined salamander, *Eurycea guttolineata* Holbrook, 1838, (formerly *E. longicauda guttolineata*) was raised to specific status by CARLIN (1997). This species has a bi-phasic life cycle (CONANT & COLLINS, 1991; DUELLMAN & TRUEB, 1994) and inhabits a wide variety of seepage, spring, river swamp, and creek systems in the eastern United States (CONANT & COLLINS, 1991). The life-history traits of *E. guttolineata* and *E. longicauda* have been studied in a variety of geographic locations. The traits of larvae and just metamorphosed specimens of *E. guttolineata* from a spring-fed marsh in North Carolina were described by BRUCE (1982), while some of the developmental and reproductive characteristics from a flood plain population in Florida were described by GORDON (1953). A detailed life-history study of *E. longicauda* inhabiting temporary ponds in New Jersey was conducted by ANDERSON & MARTINO (1966). IRELAND (1974) described the life-history traits of *E. l. melanopleura* from a spring-fed pond in Arkansas.

The previously studied populations of *E. guttolineata* were located largely in ephemeral habitats. I examined a population of *E. guttolineata* that inhabits an annually invariant, stenothermic spring ecosystem in the coastal plain of northern Mississippi, USA. The goals of my study were to describe the life-history traits of this spring-dwelling population of *E. guttolineata*, compare the findings to the results from other populations, and evaluate the influence of intra- and interspecific variation on the evolution of life-history characteristics among members of the *Eurycea longicauda* complex.

## MATERIALS AND METHODS

The study site was Poplar Cove, an approximately 50 m<sup>2</sup> spring, located at The University of Mississippi Biological Field Station in the North-Central Hills physiographic province of

Lafayette County, Mississippi, USA. Year round, the spring was stenothermic ( $x \pm s = 16.9 \pm 1.8^\circ\text{C}$ ), with dissolved oxygen levels ranging from 0.7 to 9.4 ppm ( $x \pm s = 7.28 \pm 1.79$  ppm). Water depths ranged from 0.005 to 0.100 m ( $x \pm s = 0.033 \pm 0.02$  m). The area surrounding Poplar Cove Spring (PCS) was a mixed pine-hardwood forest comprised of short-leaf pine (*Pinus echinata*), eastern red cedar (*Juniperus virginiana*), blackjack oak (*Quercus marilandica*), southern red oak (*Q. falcata*), water oak (*Q. nigra*), white oak (*Q. alba*) and sycamore (*Platanus occidentalis*). The immediate area of the spring had a canopy dominated by tulip poplar (*Liriodendron tulipifera*), an understory of American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), giant cane (*Arundinaria gigantea*), American holly (*Ilex opaca*), and the herbaceous plants netted chain-fern (*Woodwardia areolata*) and lizard's tail (*Saururus cernuus*). At this site, *E. guttolineata* co-occurred with several other caudates, including the southern two-lined salamander (*E. cirrigera*), the red-spotted newt (*Notophthalmus viridescens*), the Mississippi slimy salamander (*Plethodon mississippi*), the red salamander (*Pseudotriton ruber*) and the lesser siren (*Siren intermedia*), although the latter two species were rarely seen.

I installed a 35 m long drift fence constructed of 0.61 m wide aluminum flashing. The fence began at the point of emergence of the spring and lay approximately 4 m from the spring's margin. The drift fence bordered approximately three-fourths of the total margin but did not impede water flow. The bottom of the fence was buried to a depth of 0.10 m. The fence was supported at 3.0 m intervals with two 0.50 m lengths of 0.02 m diameter PVC piping fastened by plastic electrical ties. I placed pitfall traps adjacent to, and on each side of, the fence at approximately 3.0 m intervals, with single-ended funnel traps placed at the ends because of soil saturation in those locations. Coverboards (0.62 × 0.19 × 0.025 m wooden planks) were then placed in between pitfall traps at certain locations along the fence. The pitfall traps were 944 ml plastic buckets (0.115 m in diameter) with a 0.025 m internal lip to help prevent escape (sensu DODD & SCOTT, 1994).

Daily surveys of the drift fence were conducted from April 1995 to December 1996. As this research was part of a larger life-history study on caudates, *E. guttolineata* measurements were taken rarely during 1995. However, more thorough measurements were taken during 1996. In addition to the daily surveying along the drift fence at PCS, samples of aquatic and terrestrial salamanders were collected in May, July, August and November 1996. The aquatic samples were conducted with the aid of a dip net. The terrestrial samples were taken with the aid of a potato rake for searching through ground litter. The time spent surveying the aquatic (180 min) and terrestrial (60 min) habitats was relative to their total area (i.e., the aquatic and terrestrial habitats were 50 and 17 m<sup>2</sup>, respectively). This method was used to reduce the bias of sampling any particular area unequally. All survey data were used for determining activity, sizes, ages and months of metamorphosis and sexual activity.

I determined mean body sizes (to the nearest 0.01 mm SVL) of larvae, juveniles and adults on a monthly basis. Reproductive status of adults was determined by the presence of yolked oocytes in females (seen through the venter) and secondary sexual characteristics, such as nasal cirri and mental glands, in males (ARNOLD et al., 1993; DUELLMAN & TRUEB, 1994). I compared SVL of just metamorphosed and adult individuals within and between years with the Mann-Whitney *U* and Kruskal-Wallis *H* tests (ZAR, 1984). Size classes of individuals were established from the monthly data.

Based on the size class data from the monthly samples at PCS, ages were estimated and then assigned for each individual. This was accomplished by utilizing the three size classes of individuals (see fig. 1a and 2b, May-August) and assigning ages between 0 and 11 months for the first, 12 and 23 months for the second, and 24 and 35 months for the third size class, respectively. Larval hatching was assumed to occur in January based on the presence of a few newly hatched larvae at PCS. Larvae found in January were assigned an age of zero month. Although there may be some error in the estimates of older age classes (i.e.,  $\geq 31$  months of age), this technique provides an adequate method for assigning respective ages of larval, juvenile and subadult salamanders with non-overlapping size classes (BRUCE, 1988; STEARNS, 1992).

I estimated growth rates by regressing month of capture versus size (SVL) for each size class of individuals (ZAR, 1984). A general model of growth over the first 35 months of life was estimated by regressing estimated age versus SVL. This approach allowed for the general assessment of larval period, juvenile period, age and size at metamorphosis, and age and size at sexual maturity. I then compared these life-history characteristics to those of other populations of *E. guttolineata* and *E. longicauda*.

I utilized a Haldane coefficient of variation analysis for samples, i.e.,  $V_H = (1 + 1/4n)(s/x)$ , to determine differences in variation of age and size at metamorphosis among populations of the *E. longicauda* complex. This analysis corrects for the bias of small sample size and the effects of sampling (HALDANE, 1955; SOKAL & BRAUMANN, 1980; DELAUGERRE & DUBOIS, 1985). A *F* ratio test was used to determine statistical significance between coefficient of variation values (LEWONTIN, 1966). Assumptions of normality were met for all analyses. Finally, the relationships between larval growth rate, size at metamorphosis, and age at metamorphosis, were assessed intra- and interspecifically among populations of the *E. longicauda* complex. Growth rates were estimated using BEACHY'S (1995a) equations. Relationships were evaluated using regression and correlation coefficient analyses (ZAR, 1984). Statistical significance was set at  $\alpha = 0.05$ .

## RESULTS

The population structure of the 1995 ( $n = 48$ ) and 1996 ( $n = 61$ ) samples of *E. guttolineata* from PCS revealed two juvenile age classes prior to the first adult age class (fig. 1b). Mean sizes for each age class and month are presented in tab. 1. A few newly hatched larvae were collected in January 1995, although not measured. Larvae were present at PCS through May (tab. 1). I found that metamorphosis occurred in June and July (tab. 1). This corresponds to an age at metamorphosis of 5-6 months, assuming hatching occurred in January. After metamorphosis, the juvenile period lasted 17-19 months.

The data on sexually mature individuals (tab. 1) indicated a late summer to late autumn (July-October) period of sexual activity, with the smallest females becoming sexually active during the latter part of the season (see tab. 1, October and December). The smallest female at sexual maturity was 50.5 mm SVL. I estimated the age of this individual to be 23 months. Therefore, age at first reproduction is reached at the end of the second year of life at 22-

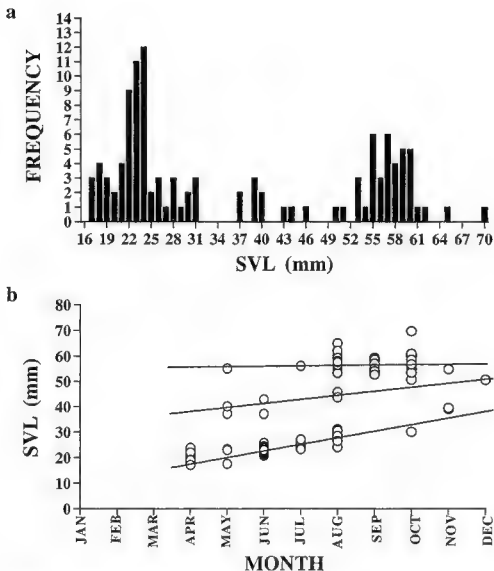


Fig. 1 (a) The frequency distribution of snout-vent lengths (SVL) of *Eurycea guttolineata* from the 1995 and 1996 pooled data from Poplar Cove Spring in Lafayette Co., Mississippi, USA. The three designated size classes are 17-31 mm, 37-46 mm and 50-70 mm SVL. (b) The pooled population structure of the 1995 ( $n = 48$ ) and 1996 ( $n = 61$ ) monthly samples of *E. guttolineata*. Growth rates are based on the regression slope for first and second year juveniles, as well as the adult estimate (solid lines). The regression analyses for each growth period were as follows: first year growth, slope = 2.48,  $r^2 = 0.84$ ,  $df = 65$ ,  $F = 326.79$ ,  $P = 0.0001$ , second year growth, slope = 1.70,  $r^2 = 0.82$ ,  $df = 7$ ,  $F = 27.41$ ,  $P = 0.0019$ , adult estimate, slope = 0.11,  $r^2 = 0.001$ ,  $df = 37$ ,  $F = 0.04$ ,  $P = 0.8356$ .

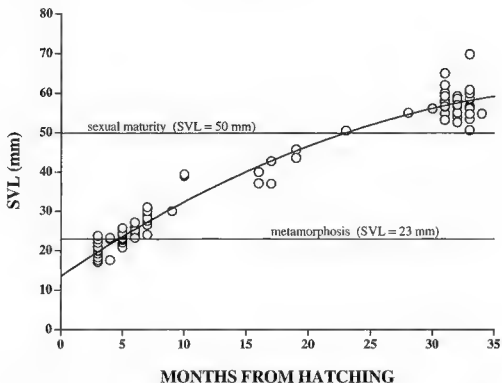


Fig. 2 A general growth model for *E. guttolineata* ( $n = 109$ ), from the pooled data of 1995 and 1996. This model incorporates timing of metamorphosis and sexual maturity. Individual salamanders were assigned an age based on their size and month of capture. These age classed data were then used to generate this growth model. A second order polynomial regression was used to generate this model. The model is:  $\text{size (SVL)} = 0.023 \text{ age}^2 + 2.121 \text{ age} + 13.506$ ,  $r^2 = 0.971$ .

24 months of age. However, the majority (85%) of sexually mature individuals were probably at least 30 months of age with a  $\text{SVL} \geq 55.00$  mm. The grand mean, standard deviation, range and coefficient of variation ( $V_{H1}$ ) for size (mm SVL) of sexually mature individuals are as follows: males,  $n = 23$ ,  $\bar{x} \pm s = 56.99 \pm 2.12$ , range 52.60-60.80,  $V_{H1} = 3.79$ ; females,  $n = 14$ ,  $\bar{x} \pm s = 58.29 \pm 5.35$ , range 50.50-69.80,  $V_{H1} = 9.51$ . Females exhibited significantly more variation in size than males ( $F_{14,23} = 5.95$ ,  $P < 0.001$ ). Egg-laying probably occurred from November to January based on the disappearance of females during late autumn and the presence of new hatchlings in January (although I observed no egg masses).

There was no difference in size at metamorphosis between samples from June 1995 and 1996 (1995,  $n = 25$ ,  $\bar{x} \pm s = 22.98 \pm 1.09$ , range 20.76-25.32, 1996,  $n = 3$ ,  $\bar{x} \pm s = 23.94 \pm 1.93$ , range 21.89-25.71;  $U = 23$ ,  $P = 0.2815$ ). There was also no difference in grand mean female SVL between 1995 and 1996 samples (1995, see tab 1; 1996,  $n = 9$ ,  $\bar{x} \pm s = 56.65 \pm 5.94$ , range 50.5-69.8,  $U = 8$ ,  $P = 0.0532$ ). Sexually active males in the 1996 sample exhibited no monthly differences in mean SVL ( $H = 2.24$ ,  $df = 2$ ,  $P = 0.327$ ). The lack of significant differences

Table 1. - SVL (in mm) for each age class of *Eurycea guttolineata* for each month of 1996. For each sample, the table gives  $x \pm s$ , followed by  $n$  in parenthesis. Data are from Poplar Cove Spring, Lafayette County, Mississippi, USA. *Italics*, data from the 1995 sample only. **Bold**, pooled data from 1995 and 1996.

Age class	April	May	June	July	August	Septem.	October	Novem.	Decem.
Larvae	<i>19.51</i> $\pm 2.08$ (16)	<i>23.09</i> $\pm 0.21$ (2)	-	-	-	-	-	-	-
1st year juveniles	-	-	<b>23.08</b> $\pm 1.19$ (28)	25.06 $\pm 1.53$ (5)	28.62 $\pm 2.21$ (10)	-	30.03 $\pm 0.00$ (1)	39.20 $\pm 0.28$ (2)	-
2nd year juveniles	-	39.04 $\pm 1.66$ (3)	39.93 $\pm 4.05$ (2)	-	44.67 $\pm 1.50$ (2)	-	-	-	-
Adult males	-	-	-	-	56.12 $\pm 1.79$ (6)	56.97 $\pm 2.09$ (9)	58.05 $\pm 2.26$ (7)	54.74 $\pm 0.00$ (1)	-
Adult females	-	55.00 $\pm 0.00$ (1)	-	56.07 $\pm 0.00$ (1)	61.25 $\pm 2.33$ (5)	54.00 $\pm 0.00$ (1)	58.21 $\pm 6.67$ (6)	-	50.50 $\pm 0.00$ (1)

between the 1995 and 1996 samples justified pooling these data for use in growth analyses (SOKAL & ROHLF, 1995).

The solid lines in fig. 1b represent growth rates for first and second year juveniles, and adults. The first year rate of growth (2.48 mm SVL/month) incorporates both larval and juvenile growth (see fig. 1b and tab. 1 for data). The y-intercept of the first year growth equation (11.21 mm) closely estimates published SVL data for hatchlings of *E. guttolineata* from other populations (GORDON, 1953; ANDERSON & MARTINO, 1966; BRUCE, 1970, 1982). Second year growth (1.70 mm SVL/month) decreased from the first year, while estimated adult growth was minimal (0.11 mm SVL/month). The combined rate of growth for juveniles, i.e., from metamorphosis to sexual maturity, was 1.49 mm SVL/month. I generated a predictive growth model for *E. guttolineata*, based on estimates of age and measures of size, that incorporates timing of metamorphosis and maturity (fig. 2).

I summarized life-history data on size, age and timing of metamorphosis from 10 populations within the *E. longicauda* complex (tab. 2). Age at metamorphosis data from each population incorporated potential variation from egg-laying dates. Using these data, I calculated the Haldane coefficient of variation for both age and size at metamorphosis. The mean data for size (tab. 2) were not different from the raw data with respect to the mean or variance ( $t = 0.95$ ,  $df = 127$ ,  $P = 0.344$ , mean data,  $n = 10$ ,  $V_{Hsize} = 9.53$ ; raw data,  $n = 119$ ,  $V_{Hsize} = 8.54$ ;  $F_{10,119} = 1.293$ ,  $P > 0.50$ ). I used data from the first year's metamorphosing

Table 2. - Data on metamorphosis for populations of the *Eurycea longicauda* complex. *E. g.*, *E. guttolineata*; *E. l. l.*, *E. l. longicauda*; *E. l. m.*, *E. l. melanopleura*. SM, size at metamorphosis (mm SVL). AM, age at metamorphosis (months) Rate, larval growth rate (mm/month). MM, month(s) when metamorphosis occurs. Perm, permanent habitat type. Ephl, ephemeral habitat type. *Italics*, standard deviation from a larval sample with same size range as just metamorphosed individuals. **Bold**, standard deviation estimated from mean and range. Sources: (1) this study; (2) BRUCE, 1982 (Caney Fork); (3) BRUCE, 1970: (3a) Cox Cove, (3b) Horse Cove; (4) GORDON, 1953, (5) SINCLAIR, 1951, (6) ANDERSON & MARTINO, 1966, (7) FRANZ & HARRIS, 1965; (8) IRELAND, 1974; (9) RUDOLPH, 1978.

Species	State county	n	SM: $\bar{x} \pm s$ (range)	AM: $\bar{x}$ (range)	Rate	MM	Habitat	Source
<i>E. g.</i>	MS: Lafayette	28	23.08 $\pm$ 1.19 (20.71-25.71)	5.50 (5.0-6.0)	2.378	Jun-Jul	Perm	1
<i>E. g.</i>	NC: Jackson	9	25.70 $\pm$ 0.71 (25.00-27.00)	4.50 (4.0-5.0)	3.044	Jul-Aug	Perm	2
<i>E. g.</i>	NC: Jackson	5	24.40 $\pm$ 0.89 (23.00-25.00)	3.75 (3.5-4.0)	3.840	Jun	Ephl	3a
<i>E. g.</i>	NC: Macon	9	26.60 $\pm$ 2.96 (23.00-32.00)	4.50 (3.5-5.5)	3.689	Aug	?	3b
<i>E. g.</i>	FL: Jackson	1	21.00	6.50 (6.0-7.0)	1.692	Jun-Jul	Ephl	4
<i>E. g.</i>	TN: Haywood	2	23.25 $\pm$ 1.06 (22.50-24.00)	?	?	Jun	?	5
<i>E. l. l.</i>	NJ: Sussex	18	22.50 $\pm$ <b>1.15</b> (20.20-24.50)	3.50 (3.0-4.0)	3.742	Jun	Ephl	6
<i>E. l. l.</i>	MD: Garrett	15	19.50 (18.00-21.00)	?	?	Jul	Perm	7
<i>E. l. m.</i>	AR: Washington	24	25.50 $\pm$ 1.25 (23.00-28.00)	6.00 (5.0-7.0)	2.583	Jun-Jul	Perm	8
<i>E. l. m.</i>	OK: Delaware	25	24.28 $\pm$ 2.25 (19.00-29.00)	6.50 (4.0-9.0)	2.197	Jul-Oct	Perm	9
Grand means, ranges, totals		136	23.58 $\pm$ 2.19 (18.00-32.00)	5.09 (3.5-9.0)	2.720	Jun-Oct	-	-

populations only, as this was a more conservative measure of variation in age at metamorphosis. Including individuals that over-wintered, i.e., > 12 month larval period, increased the coefficient of variation for age more than size. I found that age at metamorphosis had a significantly greater coefficient of variation than size at metamorphosis within the complex ( $V_{Hage} = 24.19$ ,  $V_{Hsize} = 9.53$ ,  $F_{8,10} = 5.81$ ,  $P < 0.05$ ). Moreover, this finding was consistent when habitat type (i.e., populations occurring either in permanent or ephemeral habitats) was included in the analysis (permanent,  $V_{Hage} = 16.13$ ,  $V_{Hsize} = 5.24$ ,  $F_{4,4} = 10.09$ ,  $P < 0.05$ ; ephemeral,  $V_{Hage} = 39.35$ ,  $V_{Hsize} = 8.16$ ,  $F_{3,3} = 18.87$ ,  $P < 0.05$ ). In contrast, populations of *E. quadridigitata*, the dwarf salamander, which utilize ephemeral habitats, have significantly greater variation in size than age at metamorphosis ( $V_{Hage} = 7.37$ ,  $V_{Hsize} = 22.41$ ,  $F_{3,3} = 10.58$ ,  $P < 0.05$ , data from BISHOP, 1947, HARRISON, 1973; SIMLITSCH, 1980, DUNDEE & ROSSMAN, 1989).



Finally, I analyzed the relationships between larval growth rate, size at metamorphosis, and age at metamorphosis within and among species in the complex (fig. 3a-c). I found that among populations there was not a significant relationship between larval growth rates and size at metamorphosis ( $r = 0.46$ ,  $P > 0.20$ ;  $H_0$ :  $b = 0$ ,  $t = 1.28$ ,  $P = 0.2489$ ) and age at metamorphosis and size at metamorphosis ( $r = 0.23$ ,  $P > 0.50$ ,  $H_0$ :  $b = 0$ ,  $t = 0.57$ ,  $P = 0.5869$ ). However, there was a significant relationship between larval growth rate and age at metamorphosis among populations ( $r = 0.94$ ,  $P < 0.001$ ;  $H_0$ :  $b = 0$ ,  $t = 6.74$ ,  $P = 0.0005$ ). When the data were analyzed within species, only data from populations of *E. guttolineata* provided sufficient sample sizes. Among populations of *E. guttolineata*, there was a significant correlation between larval growth rates and size at metamorphosis ( $r = 0.85$ ,  $P < 0.02$ ;  $H_0$ :  $b = 0$ ,  $t = 1.84$ ,  $P = 0.0701$ ), larval growth rate and age at metamorphosis ( $r = 0.96$ ,  $P < 0.001$ ;  $H_0$ :  $b = 0$ ,  $t = 6.23$ ,  $P = 0.0084$ ), and age at metamorphosis and size at metamorphosis ( $r = 0.80$ ,  $P < 0.05$ ;  $H_0$ :  $b = 0$ ,  $t = 2.33$ ,  $P = 0.1018$ ). However, only the relationship between larval growth rate and age at metamorphosis was significantly different from the null hypothesis  $b = 0$  (see above). The relationships between these traits for *E. l. longicauda* and *E. l. melanopleura* are shown in fig. 3a-c.

## DISCUSSION

The life-history traits of this population of *E. guttolineata* were similar to other taxa and populations in the *E. longicauda* complex. The larval period of this population was comparable to North Carolina and Florida populations of *E. guttolineata* and a population of *E. l. melanopleura* in Arkansas, but longer than that of *E. l. longicauda* from New Jersey (tab. 2). Metamorphosis also appeared to take place at a similar time regardless of the population (tab. 2). This semi-consistent pattern of timing of metamorphosis may be a function of phylogenetic history among these closely related populations, i.e., a relatedness constraint. However, there was variation in age at metamorphosis among populations, which was significantly more variable than size at metamorphosis. Therefore, variation in age at metamorphosis could result from plasticity in growth rates, as a function of the habitat, to reach an optimal size at metamorphosis (WILBUR & COLLINS, 1973) and/or genetically based differences in age at metamorphosis among populations (BERVEN, 1982).

Previous studies suggest that the short larval period of members of the *E. longicauda* complex reflects an adaptation to uncertain/ephemeral aquatic environments (ANDERSON & MARTINO, 1966; BRUCE, 1982). To evaluate this hypothesis, some theoretical predictions should be considered. WILBUR & COLLINS (1973) stated that species that exploit certain/permanent environments should have a narrow range of sizes at metamorphosis (i.e., around an optimum) and a greater range in age at metamorphosis. This pattern should result in increased variation in age at metamorphosis (e.g., from a few months to a year). In contrast, those species which exploit uncertain/ephemeral habitats should exhibit the opposite trend (WILBUR & COLLINS, 1973). Moreover, if selection is favoring an optimal size at metamorphosis, then growth rates should only influence the time it takes to reach an optimal size. BRUCE (1982) elaborated on WILBUR & COLLINS'S (1973) model by stating that in uncertain environments slower growing larvae should metamorphose at a smaller size, as opposed to delaying metamorphosis until the optimal size is reached. These theoretical predictions

## ALYTES 16 (3-4)

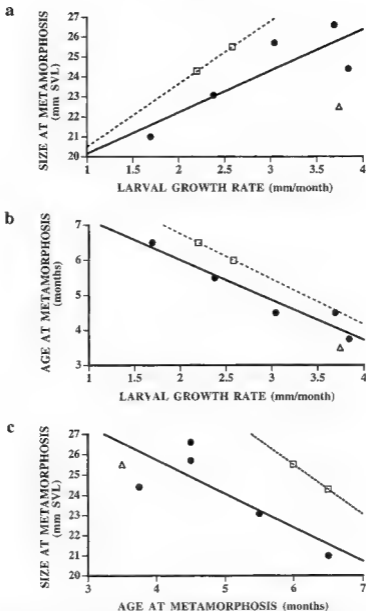


Fig 3 - Relationships between larval growth rate, age at metamorphosis, and size at metamorphosis for each member of the *E. longicauda* complex. Open squares and dashed lines, *E. l. melanopleura*, solid circles and lines, *E. guttolmeata*, open triangles, *E. l. longicauda* (a) Relationship between larval growth rate and size at metamorphosis for each species. *E. guttolmeata*, size (SVL) = 2.075 rate + 18.078,  $r^2 = 0.718$ , *E. l. melanopleura*, size (SVL) = 3.161 rate + 17.336 (b) Relationship between larval growth rate and age at metamorphosis. *E. guttolmeata*, age (months) = 1.139 rate + 8.256,  $r^2 = 0.928$ , *E. l. melanopleura*, age (months) = 1.295 rate + 9.346 (c) Relationship between age and size at metamorphosis. *E. guttolmeata*, size (SVL) = 1.664 age + 32.393,  $r^2 = 0.645$ , *E. l. melanopleura*, size (SVL) = -2.440 age + 40.140.

provide the basis for my evaluation of the hypothesis of an adaptation to uncertain environments for this complex.

The findings of this study, that age at metamorphosis is significantly more variable than size at metamorphosis, do not support the hypothesis of adaptation to uncertain environments. Instead, the data support the alternative prediction of WILBUR & COLLINS'S (1973) model, which states that in stable environments individuals should remain in the aquatic environment until an optimal size at metamorphosis is reached. The significant relationship (i.e., correlation coefficient and  $b$ ) between larval growth rate and age at metamorphosis, but not larval growth rate and size at metamorphosis (i.e.,  $b = 0$ ), supports the latter prediction. Both within and among species in this complex, the relationship between age at metamorphosis and size at metamorphosis was not significantly different from the null hypothesis  $b = 0$ . In addition, there is corroborating evidence that several populations within the *E. longicauda* complex have fast growing larvae that metamorphose within months of hatching and slow growing larvae that metamorphose more than 12 months after hatching (FRANZ, 1967, RUDOLF, 1978, BRUCE, 1982). Moreover, populations of *E. quadridigitata* that inhabit ephemeral habitats exhibited the opposite trend (i.e., significantly greater variation in size than age at metamorphosis). Therefore, populations of the *E. longicauda* complex meet the predictions of WILBUR & COLLINS'S (1973) model and support, at least in part, the hypothesis of selection for an optimal size at metamorphosis.

Although the data do not support the hypothesis of an adaptation to uncertain environments, the hypothesis of selection for an optimal size at metamorphosis does not address directly why members of this complex have shorter larval periods and smaller sizes at metamorphosis relative to other semi-aquatic plethodontids. One evolutionary explanation is that larvae are adapted to stable, warmer aquatic environments with increased food regimes (e.g., food availability), resulting in increased growth rates and smaller sizes at metamorphosis (BEACHY, 1995b).

Several studies have shown that increases in temperature and food result in increased larval growth rates (WILDER, 1924; STEWART, 1956; BIZLER, 1978; SEXTON & BIZLER, 1978; BEACHY, 1995b). However, a conflict, over the influence that increased temperature has on size at metamorphosis, has arisen between alternative models of metamorphosis. SEXTON & BIZLER (1978) stated that increases in temperature should result in shorter larval periods and smaller sizes at metamorphosis. However, JUTERBOCK (1990) stated that temperature influences on growth are not consistent among plethodontids (e.g., that sometimes decreases in temperature result in smaller sizes at metamorphosis). BEACHY (1995b) stated that the discrepancies could be accounted for by the complex relationship between increased temperatures and food regimes (i.e., that increases in temperature are accompanied by increases in food regimes). This complex temperature-food interaction can allow for increased larval growth rates, shorter larval periods, and a range of sizes at metamorphosis. This reconciles the question of how an optimal size at metamorphosis, facilitated by a stable environment, can be accompanied by a shorter larval period. A warmer, more stable aquatic environment would allow an optimal size at metamorphosis to be reached at an earlier age through an increased growth rate. Therefore, the data support the notion that habitat parameters (such as temperature and food) directly influence larval growth rates, which then influence the age at which an optimal size at metamorphosis is reached.

The majority of plethodontid life-history theory has centered on the genus *Desmognathus* (for a review, see TILLEY & BERNARDO, 1993). However, the dominant theory for the desmognathines, that increased adult body sizes are due to increased ages at maturation, does not hold for salamanders in the genus *Eurycea*. *Eurycea guttolineata* and its close relatives are at least 20 mm SVL larger (BRUCE, 1982, CONANT & COLLINS, 1991; this study) and become sexually mature sooner than or at the same age as other salamanders in the genus (i.e., *E. bislineata* complex). This suggests that age at maturity could not account for the differences in adult body size. Moreover, it appears that juvenile growth rate, juvenile period, and/or size at maturation, account for the differences in adult body size within this genus (MARSHALL, unpublished data). Although different taxa in the family Plethodontidae appear to be utilizing different strategies to attain larger body sizes, the influence of aquatic habitats on larval development may be consistent among genera (i.e., increases in temperature result in increase in larval growth rates). Moreover, this analysis provides evidence that intra- and interspecific variation in life-history traits is influenced by local environments, which play a critical role in shaping life-history evolution.

#### RESUMEN

La evaluación de características de la historia de vida nos permiten estimar la adaptación local y sus consecuencias correlacionadas de ajuste. El objetivo de este estudio fue describir las características de la historia de vida de una población de manantial, *Eurycea guttolineata* (Plethodontidae), para obtener un mejor entendimiento en la evolución de la historia de vida de Plethodontidae. Se encontró que la metamorfosis típicamente ocurre en junio, con un tamaño de 23.08 mm SVL, a una edad de 4-6 meses. El tamaño en la primera reproducción,  $\geq 50.00$  mm SVL, fue similar entre machos y hembras a una edad de 22-24 meses. Sin embargo, un gran variabilidad en tamaño en hembras sexualmente maduras (2 veces la variabilidad en machos) sugiere que algunas no lleguen a su madurez sexual hasta los 34-36 meses de edad. Los datos sugieren un periodo de actividad sexual del final del verano hasta el comienzo del invierno (julio a diciembre), con deposición de huevos al comienzo del invierno (noviembre-diciembre), y su eclosión en enero o febrero. Tasas de crecimiento fueron altas durante el primer (2.48 mm SVL/mes) y segundo (1.70 mm SVL/mes) años de vida, mientras que decrecieron (0.31 mm SVL/mes) una vez alcanzada la madurez sexual.

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Corresponding editor: Janalee P. CALDWELL.